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Eastern Pacific Expeditions of the New York Zoological Society. XXIX.

On the Growth and Ecology of Brachyuran Crabs of the Genus *Ocypode*.[1]

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(Plates I–II. Text-figures 1–7.)

[This is the twenty-ninth of a series of papers dealing with the collections of the Eastern Pacific Expeditions of the New York Zoological Society made under the direction of William Beebe. The present paper is concerned with specimens taken on the Eastern Pacific *Zaca* Expedition (1937–1938). For data on localities and dates of this expedition, refer to *Zoologica*, Vol. XXIII, No. 14, pp. 287–298. Also included in the present paper are results of observations made by the author on the Pacific coast of Panama during January, 1941.]

Contents

I. Introduction.

The present paper is the third of a series dealing with the brachyuran crabs of the Eastern Pacific *Zaca* Expedition. My sincere thanks go to Mr. Templeton Crocker for the opportunity of making these collections and of studying the crabs in the field, to Dr. William Beebe for his unfailing helpfulness and for leave of absence making possible a special trip to Panama, and to Miss Janet Wilson for her excellent drawings.

The references given under each of the two species discussed include the type description, Rathbun's monograph (1917), and occurrence records which have appeared since the latter date. The collection is deposited in the laboratory of the Department of Tropical Research, New York Zoological Society.

II. Summary of Important Points.

1. Young crab stages of *Ocypode gaudichaudii* and *O. occidentalis* differ from adults chiefly in the flatter, more narrow carapace, longer legs, larger eyes, more oblique orbits, smaller chelipeds and different coloration. In *gaudichaudii* the ocular stiles and truncate chelae begin to develop when the crab is less than half grown, the carapace being around 7 mm. in length when the first trace of stiles appears, and 10 mm. when the chelae tips begin to show change in form. In adult males the stile is only slightly longer than in females; this difference is not apparent in young crabs.

2. Adult *gaudichaudii* apparently alone of all the genus feeds habitually on microscopic organic matter in the sand, just as do crabs of the related genus *Uca*. In *gaudichaudii*, however, the technique differs: first, a raking motion of the truncate chelae is substituted for the pinching of sand by the pointed, spooned chelae in *Uca;* second, the specialized endites of the first maxillipeds form sand pellets which drop of their own weight, instead of being wiped off as in *Uca*. Young *gaudichaudii* habitually, and adults rarely, prey on small crustaceans, insects and worms, and sometines add wood and seaweed to

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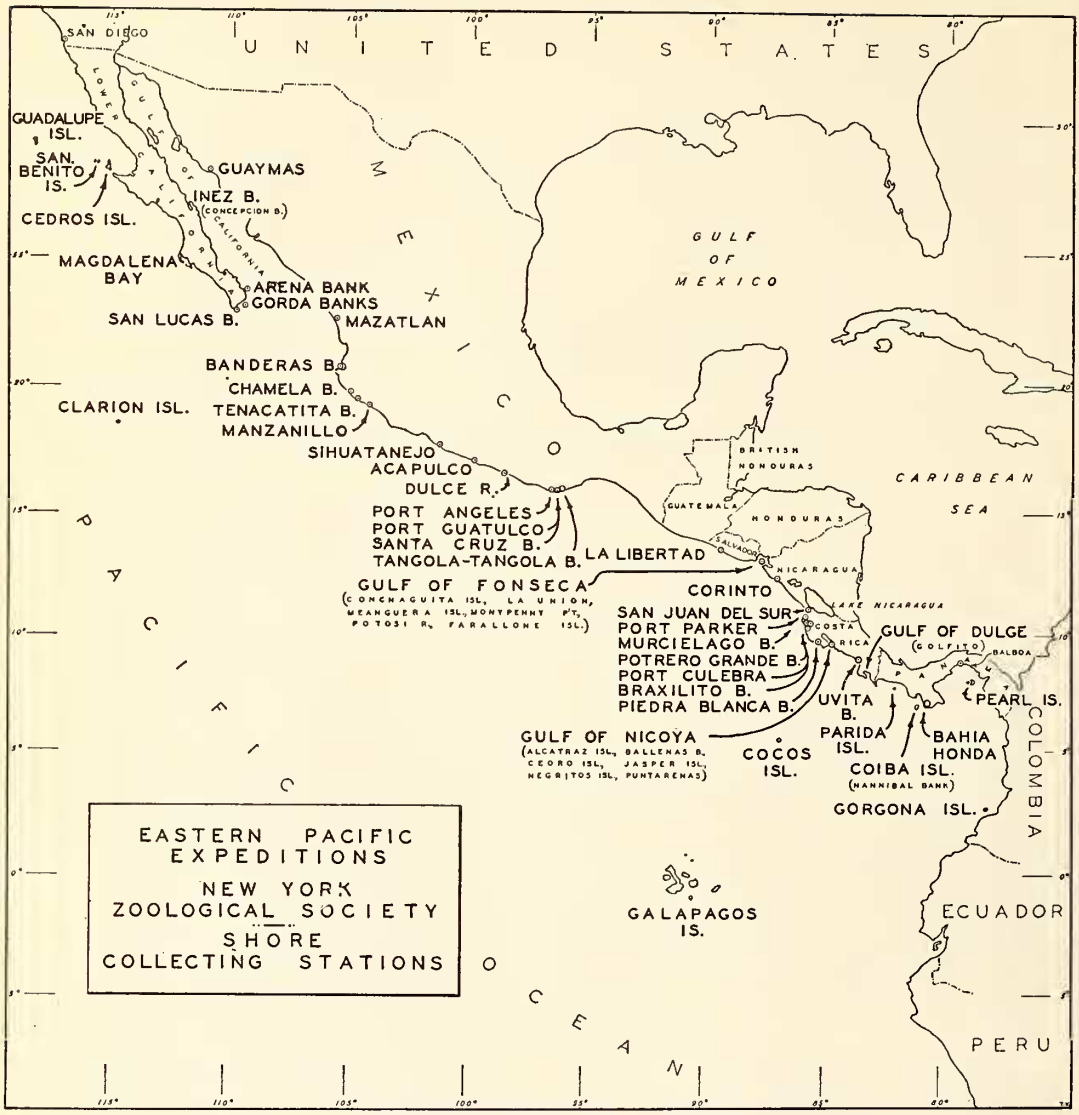


Text-figure 1.

Shore collecting stations of the Eastern Pacific Expeditions of the New York Zoological Society.

their diet. *O. occidentalis* is a predator and scavenger.

3. *O. gaudichaudii* is diurnal, *occidentalis* nocturnal except when very young.

4. In contrast to the racing dodging, burrowing adults, the young of *gaudichaudii* run only a short distance when pursued, then flatten themselves in the sand, where protective coloration aids them in escaping observation.

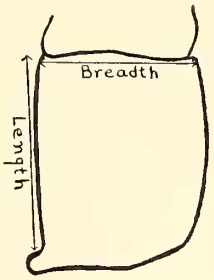
5. Also included in the present paper are descriptions of color in life, stridulation, habitat, burrows and daily schedule, with special emphasis on *gaudichaudii*. Abdominal appendages of the three American species, *gaudichaudii*, *occidentalis* and *albicans*, are illustrated.

III. Key to Immature *Ocypode* from the Eastern Pacific.

O. occidentalis and *O. gaudichaudii*, although so distinct in the adult, are superficially indistinguishable up to a length of about 7 mm., when the ocular stiles and truncate chelae of the latter species begin to develop. However, they may be distinguished when alive by color differences, and when preserved by the proportions of the buccal frame, as shown from the following key. The smallest specimens studied were about 4 mm. in length.

The length of the ischium of the third maxilliped is measured along its external margin in a straight line, as far as but not including the

basal process; the breadth of the ischium is measured across the distal margin. The accompanying diagram illustrates these points.



1a. Living crab with a spot of brilliant scarlet on middle of posterior gastric region, and others on one or more of the meri of the last three pairs of ambulatories. Breadth of ischium of third maxilliped 58 to 69 per cent of its length..... *occidentalis*, p. 308

1b. Living crab without scarlet spots. Breadth of ischium of third maxilliped 77 to 85 per cent of its length..... *gaudichaudii*, p. 209

IV. Crabs of the Genus *Ocypode* Taken by the Eastern Pacific *Zaca* Expedition.

Ocypode gaudichaudii Milne Edwards & Lucas.

Text-figs. 2; 4 A, B, C, D; 5 B, D, F, H; 6 B, D; 7 E, F; Pl. I, Fig. 1; Pl. II, Figs. 3, 4.

References: Ocypoda gaudichaudii Milne Edwards & Lucas, 1843, p. 26; 1847, pl. 11, figs. 4–4b.
Ocypode gaudichaudii, Rathbun, 1917, p. 373; pl. 129, fig. 1; pl. 130, fig. 1; Boone, 1927, p. 267, fig. 96A; 1929, pp. 562, 580; Pesta, 1931, p. 174; Sivertsen, 1934, p. 19; Crane, 1940, p. 67; text-figs. 1–8.

Range: Gulf of Fonseca, El Salvador, to Chile; Galápagos Islands.

Local Distribution: Found on more or less protected beaches and on the shores of lagoons. In one locality (Bahia Honda, Panama), there were more than 3,000 crabs on a beach measuring about 175 × 400 feet. Very rarely found on the same beach with *O. occidentalis*, and then usually one or the other species occurs in the young stages only, so that its presence is doubtless accidental.

Size: The 55 specimes in the present collection measure between 4.8 and 29 mm. in length of carapace. One of Sivertsen's (1934) males from Galápagos was 36 mm. long, and a female 34 mm.

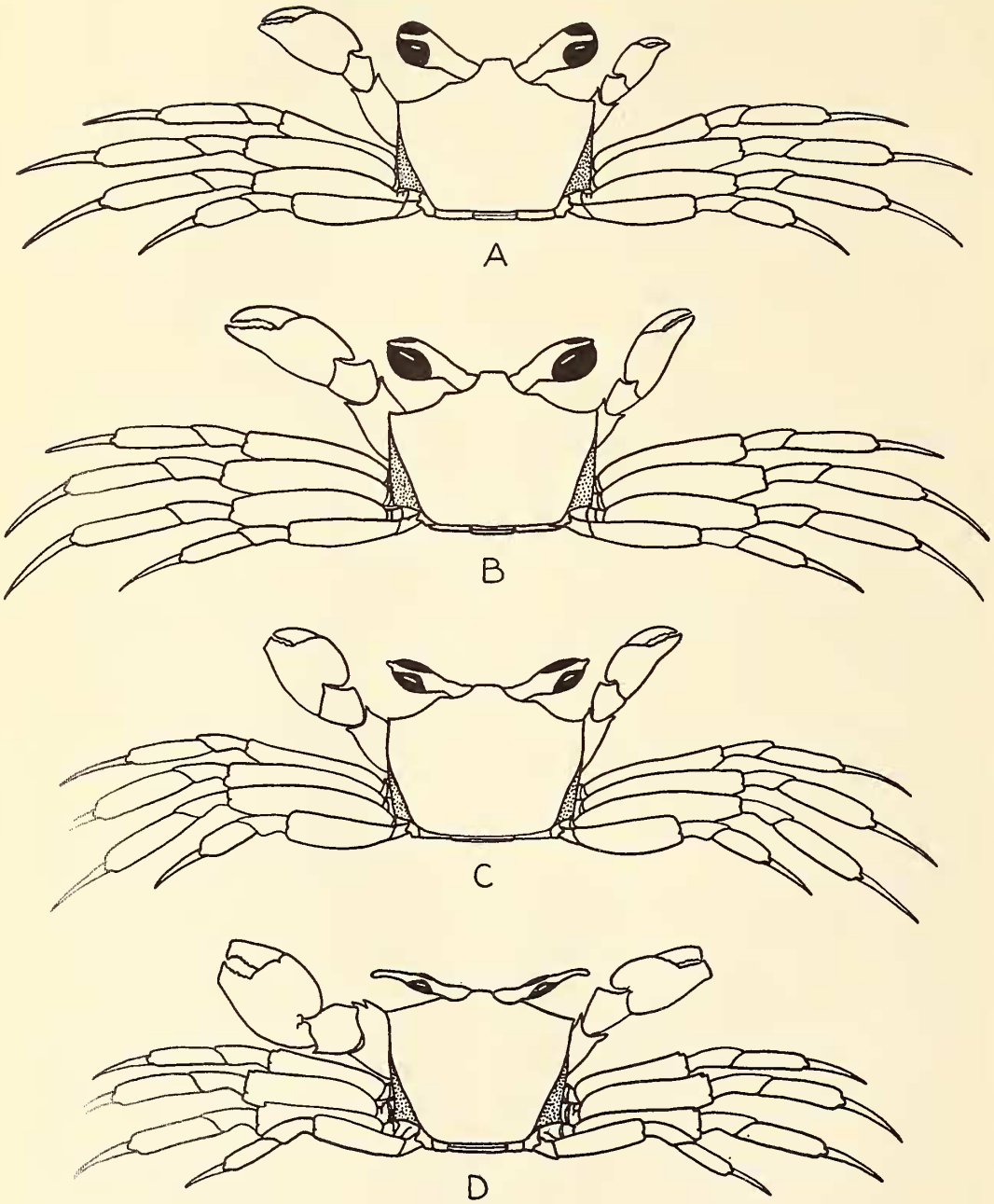
Sexual Characters: Except for the probably larger maximum size and slightly longer ocular stiles of the male, there are no apparent secondary sexual characters. The form of the abdominal appendage in this genus, as in *Uca*, varies among the species, so that it should prove a valuable taxonomic character in the determination of dubious forms. Plate II, Figs. 4, 5 and 6 illustrate the appendages of the three American species.

Color: This species ranges in general color from brilliant coral red to dark brown, marbled or mottled with brown, yellow and yellow-green. The exceedingly variable color is affected by a number of factors, including the color of the sand upon which they live and the sex and size of the individual. No precise observations have yet been made on the influence of light and temperature on the one hand, or of physical and emotional states on the other, but these will undoubtedly prove to be of great importance, and the crab found to be capable of considerable individual variation. The only exact notes taken on the latter subject concerned an ovigerous female: the sides of the carapace were gray-violet when the crab was captured on a dark, stormy day after a long chase over light sand; they changed to moderately bright coral red after two days in a box kept partly in sunshine, its bottom being covered with the same light sand. There was no color change at night. Compare especially the observations of Cowles (1908) on color change in *O. albicans*, Abramowitz & Abramowitz (1940) and Brown (1940) on the effect of eyestalk removal in *Uca*, and Crane (1941) on color change in courting *Uca*. Similar experiments and observations made upon *O. gaudichaudii* should yield interesting results.

In regard to the effect of the environment, it was obvious that crabs on light sand were brightest, with a great deal of orange, carnelian and coral pink, while those on dark, volcanic sand were darkest, with these brilliant colors replaced by browns, rusty oranges and pale pinks. In any group the adult males were brightest, the females paler, the young palest. In specimens less than about 15 mm. long, the parts that were yellow in adults were white, those that were coral or carnelian red were lavender or violet; especially noticeable in the young was a band of violet across the posterior part of the carapace.

Colors of adult males have been noted in detail as follows: ground color of carapace ranging from bright coral or carnelian red in colonies living on the palest yellow sand, through coral pink and rusty orange, to dark brown in colonies on dark slate-colored sand; carapace with mottlings or marblings ranging from pale lemon yellow or chartreuse with dark brown to ochre or chartreuse with cream and white; sides of carapace brilliant clear orange to scarlet orange, sometimes mottled with pink. Eye sockets brilliant orange to dark brown; stalks coral red to pearl gray; eyes pearl gray; stiles scarlet orange to yellow-brown. Merus and carpus of chelipeds orange or orange-brown above with brown mottlings, buffy yellow below and on inner surface; upper third of manus bright coral pink or orange to dark brown; lower two-thirds pinkish-white to lemon yellow; chelae coral pink, orange or lemon yellow. Posterior (dorsal) surface of ambulatories usually like carapace, but dactyls are buff when crab lives on light sand, olive green when on dark sand; anterior (ventral) surface of ambulatories usually pale. Sternum and abdomen bright coral pink, sometimes mottled carnelian red, yellow and white, sometimes fading into white posteriorly.

Early Crab Stages: Several excellent studies on the growth of *Ocypode* have already been pub-



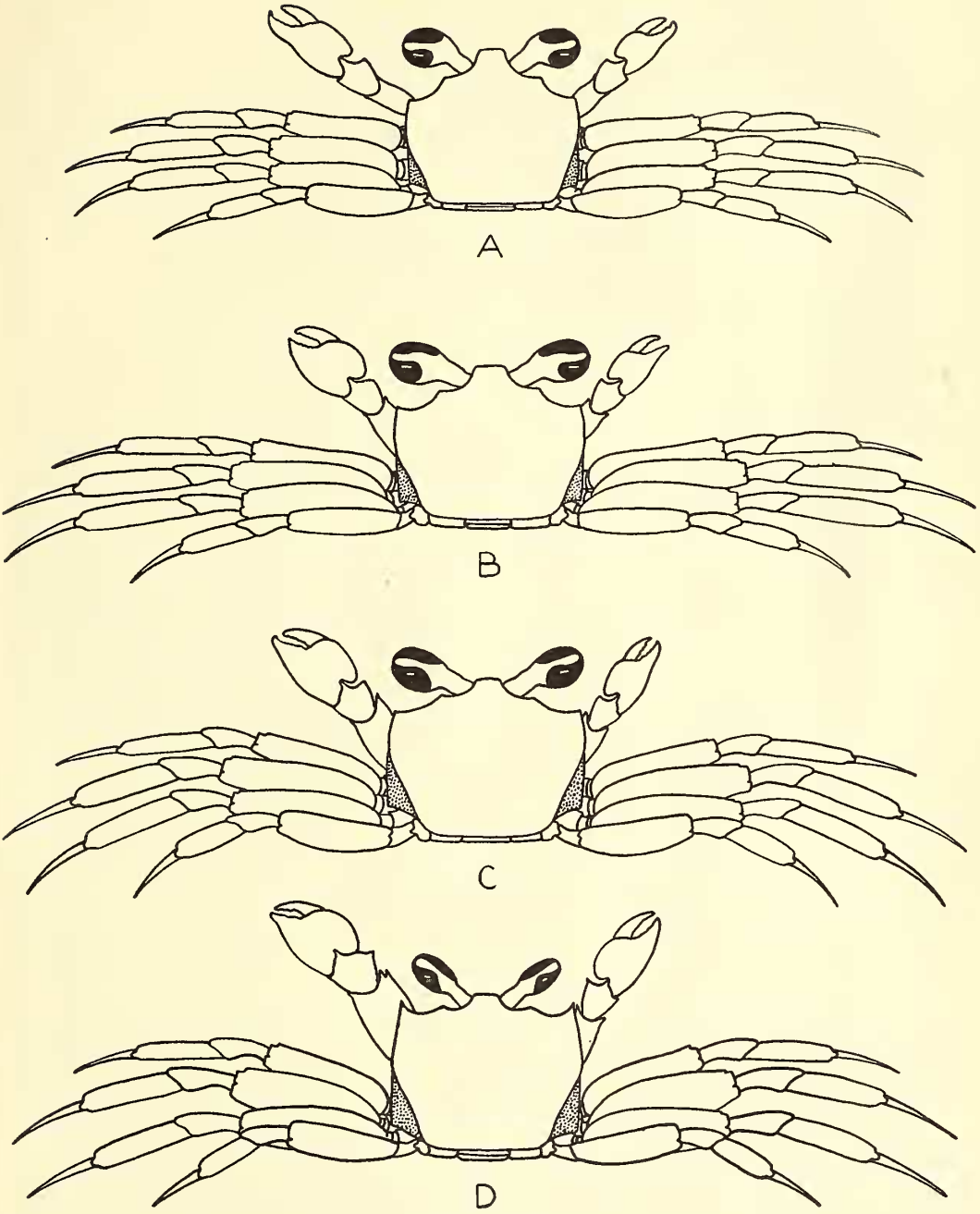
Text-figure 2.

Ocypode gaudichaudii. Growth stages. Carapace lengths: A, 4.8 mm.; B, 7.2 mm.; C, 10 mm.; D, 29 mm.

lished, notably those of Cott (1929), Huxley (1931) and Sandon (1937). It seems worthwhile, however, to summarize and illustrate the changes occurring during growth in *gaudichaudii*, especially since this species is more specialized than others studied (*ceratophthalma* and *aegyptica*).

The changes in *gaudichaudii* were studied from a series of 64 specimens ranging in length from 4.8 to 29 mm., the carapace being measured in the median line. The outstanding growth characters of the young are as follows, all of the observations being of course relative to the size of the crab.

1. The carapace is broader than in the adult,



Text-figure 3.

Ocypode occidentalis. Growth stages. Carapace lengths: A, 4.2 mm.; B, 6.9 mm.; C, 10 mm.; D, 25 mm.

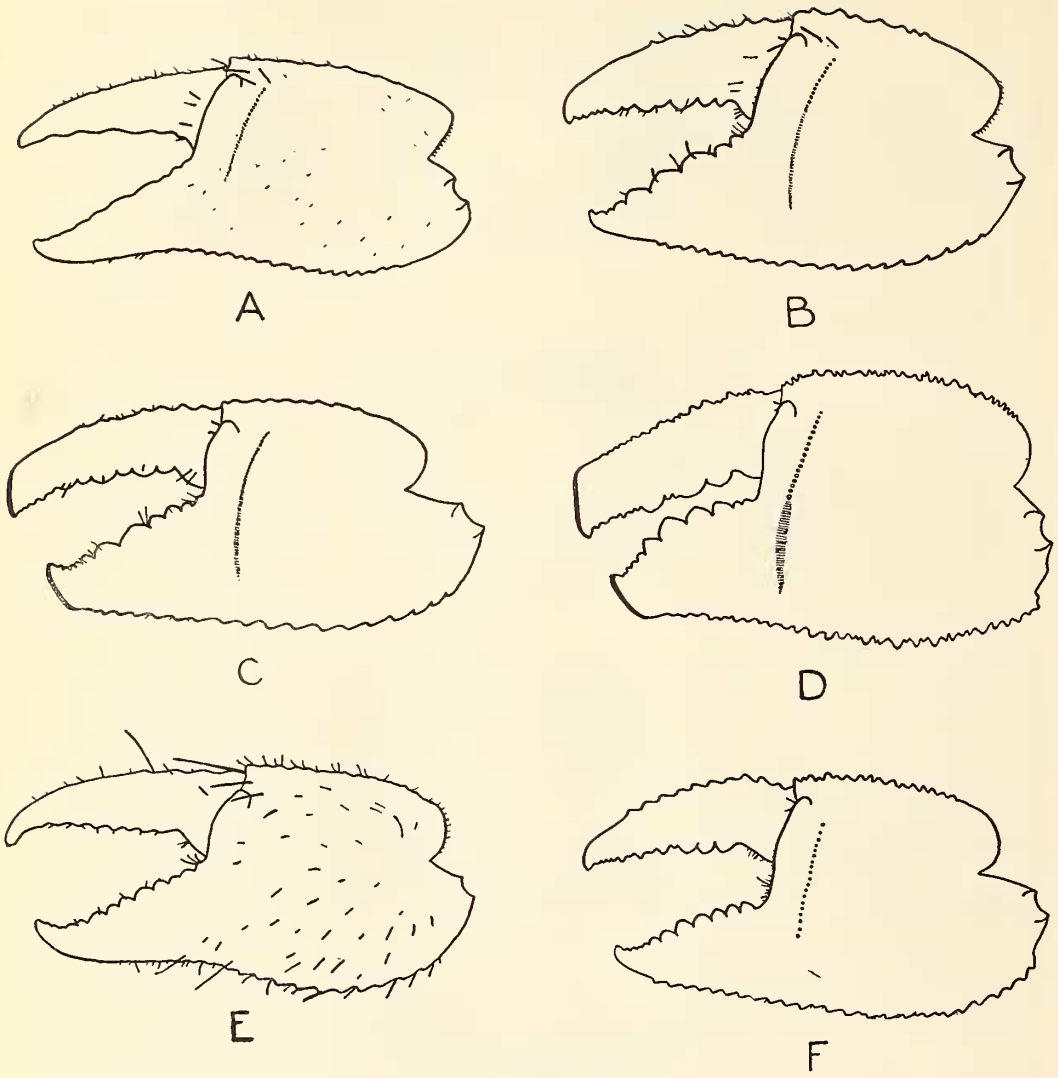
breadth being greatest when the crab is about 7 mm. long.

2. The carapace is less deep.

3. The orbits are more oblique.

4. The eyes are enormous, being broader and thicker as well as longer.

5. The eyestalks are longer and thicker, but there is no trace of stiles until the crab reaches a length of about 7 mm. In their early stages, the stiles are equipped distally with a few hairs, as in adults of certain other *Ocypode*. The stiles will be further discussed below.



Text-figure 4.

Major chelae of *Ocypode*. A to D, incl., *gaudichaudii:* A, female, carapace length 4.8 mm.; B, female, carapace length 7.2 mm.; C, male, carapace length 10 mm.; D, male, carapace length 29 mm. E, F, *occidentalis:* E, female, carapace length 4.2 mm.; F, male, carapace length 25 mm.

6. All the joints of the chelipeds are more slender, the width of the manus being only three-fourths that of the grown crab in a specimen 4.8 mm. long.

7. The chelae show the first signs of truncation when the crab reaches a length of about 10 mm.

8. A stridulating ridge is present even in the smallest (4.8 mm.) crabs, but is composed only of minute, homogeneous granules, instead of having parallel, elevated lines in its upper half. In these smallest examples the inside of the palm is slightly hairy.

9. The ambulatories are relatively longest when the crab is about 7 mm. in length.

10. The colors of the young have already been noted (p. 299).

11. The crabs appear, anatomically, to reach maturity at a length of around 22 to 24 mm.; this point cannot, however, be settled until more is known of their breeding habits. The only ovigerous female taken measured 27.5 mm. in length.

Stiles: A number of writers (for example, Ortmann, 1894, p. 768, Lanchester, 1900, p. 759, and Gordon, 1934, p. 9) have mentioned the fact that in other species of *Ocypode* furnished with ocular stiles the latter are absent in the young and reach their maximum development in large

males. In. *O. ceratophthalma,* stiles do not begin to develop much before a length of 20 mm. is reached (Lanchester, *ibid.*), in contrast to *gaudichaudii,* in which, as has been said, stiles are first visible at a length of about 7 mm. In *gaudichaudii,* too, the sexual difference in stile length is relatively slight, and is not apparent at all until the crab measures about 20 mm. Indeed, in smaller crabs, the stiles on the average are even slightly shorter in males than in females. In both sexes, the stile grows more rapidly after the crab has reached a length of about 20 mm. The following table is based on a series of 31 males and 23 females.

Length of carapace in mm.	*Length of stile in mm.*	
	Males	*Females*
4.8 to 6.6	Absent	Absent
7 to 14	0.2 to 1.2	0.1 to 1.0
15 to 19	1.1 to 1.9	1.3 to 2.4
20 to 24	2.4 to 4.3	2.4 to 3.5
25 to 29	4.6 to 7.5	3.2 to 5.5

Largest male, 29 mm. long, stile length 7.5 mm.
Largest female, 27.5 mm. long, stile length 5.5 mm.

Dembowski's detailed description (1913) of the glandular organs of the ocular stile and stalk of *ceratophthalma* has apparently not been superceded, while Parenzan (1931) ascribed to the stiles of the same species a tactile and protective function in addition to their glandiferous capacity. It will be interesting to study in detail the functions of both stiles and glands, and to determine whether the latter control chromatophore expansion, as do the sinus glands in the eye-stalks of *Uca* and other crustaceans (see for example Abramowitz & Abramowitz, 1940; Brown, 1939; and Kleinholz & Bourquin, 1941).

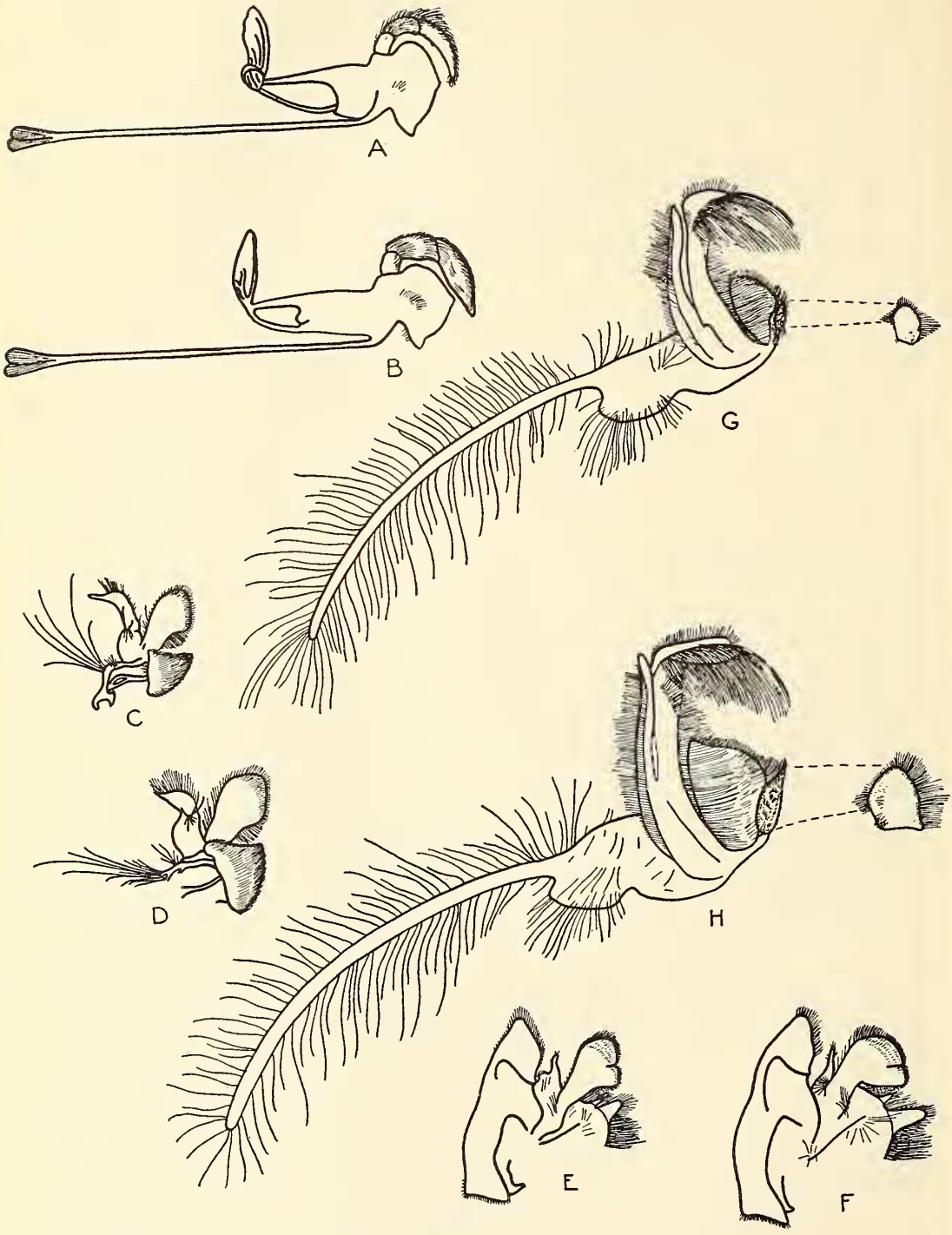
Food, Feeding and Mouthparts: Unlike other members of the genus, which are confirmed predators and scavengers in the usual sense of the word, *gaudichaudii,* except when very young, feeds almost entirely on microscopic organic matter washed onto the sand by the tide, exactly as does *Uca.* As in the latter genus, the minute particles of animal and vegetable matter are gathered by sifting pinches of sand through the mouthparts and dropping the remaining sand in small pellets from the posterior part of the buccal region. In feeding, alternate claws are used, at the rate of four scoops to the second; pellets emerge at two to the second. Rejected pellets of large crabs measure on the average one-quarter to three-eighths of an inch in length and are broadly oval.

The details of the method by which the food is gathered, although analogous to the procedure in *Uca,* are in *O. gaudichaudii* unique. In *Uca* the minor chelae are spooned, and literally pinch up clawsful of sand, the dactyl being widely extended before every pinch. In *O. gaudichaudii,* the sand is not picked up between the chelae, but instead the latter are held almost closed, and used simply as broad-toothed rakes, scraping backward, inward and upward. The inner surfaces of both dactyl and pollex are slightly concave, and this characteristic, combined with their truncate tips, must make them almost or quite as efficient sand-gatherers as the entirely different chelae of *Uca.* Each scoop of sand, as in *Uca,* is swiftly lifted to the anterior end of the buccal cavity, where it is swept from the chelae by the palps of the third maxillipeds. No way has yet been found of watching exactly how the organic matter is separated inside the mouth, although as in similar observations on *Uca* the parts can be seen to be in rapid motion.

Whatever the details of manipulation in *gaudichaudii,* it is apparent that the sand about to be rejected is formed into a pellet in the middle of the lowest (most posterior) part of the buccal cavity, between the enlarged endites of the first maxillipeds. The pellet is not wiped off by the chelae, as in *Uca,* nor does the sand simply accumulate outside haphazardly and drop by means of gravity; instead, it appears to be carefully moulded into a pellet, by the up-and-down motion of the endites, and dropped. Since damp sand lacks much of the stickiness of mud, such a procedure is practicable in this crab, whereas it would be impossible in most *Uca,* which are largely mud-feeders (cf. Crane, 1941). The technique of separation is not perfect, since small amounts of sand are usually found mixed with the organic matter in the alimentary canal.

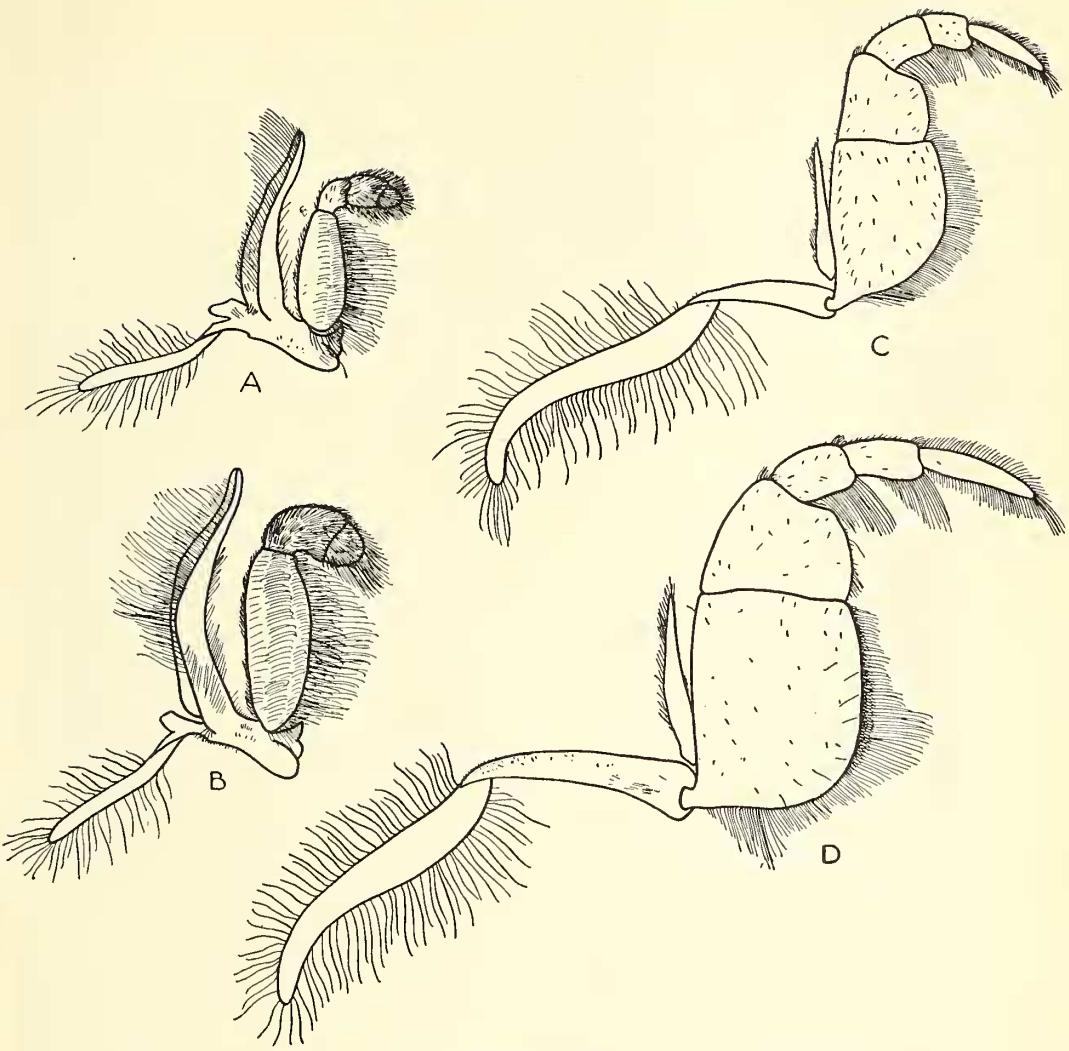
A comparison of the mouthparts of *gaudichaudii* with those of *occidentalis* is enlightening. The latter in feeding habits is a typical *Ocypode,* the west coast analogue of *albicans,* and feeds on the usual assortment of seaweed, carrion, amphipods, insects, etc. I have never seen it put sand into its mouth, and have rarely found grains in its stomach.

In *gaudichaudii,* the entire mouth field is much larger than in *occidentalis,* ranging from 25 to 30 per cent. more in both length and width, and with the parts correspondingly larger, a condition which is apparently useful in manipulating large quantities of sand. In *gaudichaudii,* too, the hairs on the mouthparts are much longer and thicker, although not as long as in mud-living *Uca*'s, where even more straining work is necessary than in sand-living *Ocypode.* Specifically, the hairs on the inner margins of the third maxillipeds are up to more than three times as long, and those on the second maxilliped one and a half times to twice as long. The maxillae are also larger and tougher and the mandibles slightly longer. There are no pectinated spoon-tipped hairs, so characteristic of most fiddler crabs, on the second maxilliped of either species of *Ocypode;* in both, however, there is a row of short, thickened hairs on the inner (dorsal) side of the merus and a cluster of similarly thickened and slightly concave hairs among the normal ones on the tip of the palp; these stout hairs are slightly longer and more numerous in *gaudichaudii* than in *occidentalis.* The anterior margin of the sternum is broader in *gaudichaudii,* squared off and slightly concave, perhaps for better retention of the sand during manipulation, while



Text-figure 5.

Mouthparts of *Ocypode.* A, mandible, *occidentalis;* B, same, *gaudichaudii;* C, first maxilla, *occidentalis;* D, same, *gaudichaudii;* E, second maxilla, *occidentalis;* F, same, *gaudichaudii;* G, first maxilliped, *occidentalis;* H, same, *gaudichaudii.* All × 4.1, from ♂'s 25 mm. long.



Text-figure 6.

Mouthparts of *Ocypode*. A, second maxilliped, *occidentalis;* B, same, *gaudichaudii;* C, third maxilliped, *occidentalis;* D, same, *gaudichaudii*. All × 4.1, from ♂'s 25 mm. long.

in *occidentalis* this area is narrower, sloping and convex.

The most interesting of the differences, however, lies in the development of the proximal endites (basipodites) of the first maxillipeds. In *Ocypode* as in *Uca* there is considerable space between the anterior tip of the sternum, which extends upward between the maxillipeds, and the mandibles. In *gaudichaudii*, however, there is twice as much as in *occidentalis*, in which the extra space is negligible. In *gaudichaudii* this extra space is occupied chiefly by the proximal endites of the first maxillipeds—which, instead of lying almost useless on each side of the sternal projection, with their flat sides turned backward against the sternum (as in grapsids, portunids, etc.), are in *gaudichaudii* and *Uca* enlarged, thickened, and their flat surfaces closely opposed to each other, exactly like a pair of butter-ball paddles. The distal endites (coxopodites) and the maxillae, in normal position, thus support and strengthen them laterally, instead of being anterior to them. In *occidentalis* the general form and position of the proximal endites are almost the same, but they are so small and weak, and there is so little space for them that they obviously could not function as paddles.

An examination of a series of alimentary tracts combined with observation in the field, showed first, that feeding habits changed with growth and, second, that large crabs occasionally varied their planktonic diet with other items. Twenty-one stomachs and intestines were examined, from crabs measuring between 5 and 29 mm. in length, taken in eight different localities. This series divided itself naturally into two parts,

one including crabs less than 9 mm. in length, and the other of those longer. The seven alimentary canals comprising the first group contained no trace of sand, and the contents consisted entirely of amphipods and tiny insects, including beetles, in an easily recognizable state. Obviously at this stage, in which the chelae have not become truncate, the crabs are chiefly predators—just as they were in the megalopal stage—and, doubtless, scavengers as well. Similarly, their food is identical with that of other *Ocypode* from the young of which, physically, they are scarcely to be distinguished.

After a length of 9 or 10 mm. has been attained, however, the crabs commence feeding almost entirely by means of sifting plankton from the sand. Correlated with this is a concomitant development of the truncate chelae. As was to be expected, the stomach contents of this second group, numbering 14 crabs, consisted of particles of organic detritus, including diatoms and minute algae. Ten stomachs included more or less sand in addition. In only four was non-planktonic matter found, and in these sand was present in the intestine, showing that the unusual food was not habitual: the stomachs of two adults from the same locality held isopods and bits of wood; another had worm spicules and pieces of seaweed; and a fourth held a small crab, probably *Sesarma*. These must be regarded as exceptional; several times I have seen large colonies of *gaudichaudii* scooping up the sand, while a dead fish or bird lay untouched in their midst, although hermit crabs busily feeding on the carcass attested its worth as food to true scavengers.

I have never seen a member of this species behave as reported to Miss Rathbun (1917, p. 374) by Tristan, although I have baited them with a number of objects, edible and inedible, including both animal matter and seaweed: "If anything falls near them," wrote Tristan, "they jump at it with extraordinary rapidity, as a spider in its web, and try to secure it with their claws so as to carry it off quickly to their holes." Similarly, I have never found material of any kind in their holes.

The only mention I find of other *Ocypode* feeding in the manner of *gaudichaudii* is that of Takahasi (1935), who reports that the *young* of *ceratophthalma* and *cordimana* feed on plankton and make "sand-balls," along with *Uca*, *Scopimera*, *Ilyoplax* and *Mictyris*. It is interesting that the young of *gaudichaudii* are, in contrast, predators.

Burrows: The burrows are of three main types, and I have not been able to discover that each type is the work of a certain size or sex, or dug in a given sort of locality. The most usual form made by adults seems to be a burrow which goes 6 to 12 inches straight down, then turns at a right angle or more and continues for an almost equal distance. Other individuals, however, dig straight down for six inches, and then continue in a slow spiral. Still others dig a simple, oblique burrow about nine inches long, ending about six inches underground. To discover which, if any, is the normal type, plaster casts must be taken in a number of localities.

The method of digging agrees in general with the method used by other *Ocypode*, the sand brought up being carried by the first and second ambulatories on the side of the minor cheliped (the side which usually enters the hole first and leaves last). The minor cheliped is laid flat against the load of sand, bearing no weight, but holding it in place. Small loads may be taken two or three feet from the hole and flicked six inches still farther, being flung sideways and forward through the legs and under the cheliped of the other side. Large loads, however, which in large crabs are the usual kind, are simply dumped close to the hole.

In Panama City I noticed a habit which had not been apparent in crabs farther north. When the load has been released near the hole, the crabs deliberately stamp the sand flat with the outer sides of the palm of the chelipeds rapping alternately and quickly against the ground. Simultaneously similar motions are made by the dactyls of the first two pairs of ambulatories, which, instead of bearing the weight of the crab on their tips in the usual fashion, are turned inward, so that the weight rests on the dactyls' entire length, and more pounding surface is given. By just a few of the patting motions the heap of sand becomes almost indistinguishable from its surroundings; on the way back to the hole after an absence the crab usually continues the process, apparently to take care of any stray slippings. Also, they frequently stamp in the immediate vicinity of the hole even when they have not brought up a load.

The procedure was exactly similar to that observed in male *Uca* in preparing a smooth display ground, free from pellets and digging lumps alike, in front of its burrow. All the instances were seen on rather dry sand in January. No evidence of courting activity was seen, although it may be that this action is connected with it. It was not seen in equally detailed observation of the species at Bahia Honda, in northern Panama, in March. It may, of course, be connected only with the type of sand, but it is worth noting that it may prove to be a definite part of courtship. Among these stamping crabs a number of rudimentary fights were seen; chelae were never locked as in *Uca*, but were used only in very brief sparring matches.

In one instance, a large crab, the sex of which was not determined, stamped down a fresh load carefully, then darted eighteen inches away to the newly started hole of a smaller crab. The latter had brought up three or four loads and dumped them in as many different places, without stamping them down at all. The first crab stamped down one of the second crab's loads, then chased the animal several feet, watched it keep on running, then returned to the newly started hole and deliberately kicked sand into it

until it was almost indistinguishable from the surrounding beach. The aggressor then returned to its own hole and resumed repair work.

Defense: Crabs of this species employ four distinct types of defense mechanism, according to their size. The smallest noticed, measuring less than 8 mm. in length, are perfectly matched to the sand in color, being finely and evenly marbled with buff and black on carapace and legs. .They take every advantage of the similarity in color, since they run only a few feet, or dodge a few inches, when pursued, then flatten themselves and remain motionless on the open sand. These smallest crabs were not seen to escape down holes, even when they were at hand, and apparently had none of their own; the smallest crabs found digging burrows measured between 7 and 8 mm. in length.

If a moderate-sized crab—that is, one too small to have any orange developed dorsally—is dug up and, its hole having been destroyed, allowed to escape, it will, if pursued with moderate force, try to take refuge in a footprint or any other kind of depression in the sand, where it flattens itself and blends in color exceedingly well. However, if still pursued, it will descend any available hole.

Large crabs when pursued never depend on flattening in a depression to escape notice, which would, of course, be impossible thanks to their usually striking color, Instead. they run swiftly, in typical *Ocypode* fashion, to their own hole if possible, or, if not, to that of any neighbor; if this is impossible they dodge and double on the open sand, or seek the shelter of nearby rocks. None of this species, of any size, was seen to take to the water except for a single ovigerous female, which was apparently aërating her eggs.

Large crabs at bay employ the fourth means of defense, which, of course, is the assumption of a threatening attitude, with the nippers upraised and open, as the crab makes every attempt to pinch the attacker.

Stridulation: Alcock's (1892, p. 336) and Anderson's (1894, p. 138) observations on the use of stridulation apply equally well to this species. Whatever its other uses, if any, it certainly is a means of warning trespassers that a burrow is occupied. More than a dozen crabs of both sexes were dropped into the holes of as many others. In each case, when the ear was bent over the hole, distinct twittering squeaks were heard, especially at first. However, if I remained in position, apparently giving evidence of my presence through the shading of the hole, the two crabs always seemed to come to some sort of compromise in regard to sanctuary, the squeaking ceased, and the trespasser remained down the strange hole indefinitely. Naturally, strange large males caused the most commotion. The usual result, as found by subsequent digging, is for the newcomer hastily to dig itself a little niche in the side of the tunnel, the displaced sand forming a loose plug in the mouth. The scrape of the bodies against each other and the digging sounds can be heard, quite distinct from the stridulation. Although the latter may be imitated artificially with a crab held in the hand, it is higher pitched when performed naturally in a burrow. Presumably only the rightful owner stridulates, but this point has not been checked, as it could perhaps be in a glass-sided terrarium. If the observer retires promptly to a distance of about twelve feet, the trespasser will emerge within two minutes, and pause at the mouth for several minutes more until certain that the danger is past.

Miss Rathbun (1917, p. 374) quoted a note from Tristan regarding this species as follows: " . . . at low tide the crabs begin to come out sideways, remaining on the edge of the holes and hiding very quickly at the slightest noise." Although they are extremely sensitive to movement, my own observation and experiments indicate that noises (excluding, of course, their own stridulation) have absolutely no effect on them.

Daily Schedule: The following notes are based chiefly upon observations at Bahia Honda, Panama, on a large colony living on light sand. The beach is close to the mouth of the bay, but protected from the full strength of the surf by an island close to shore. The holes as usual were all in the upper third of the beach, and covered at high tide.

These crabs are decidedly diurnal, and their daily routine is similar whatever their habitat. An individual, upon emergence from his hole near high tide line as the water recedes, is apparently very tired, and sits beside its hole, obviously resting, leaning first on one side, then on the other. At the slightest disturbance, even the close approach of a neighboring crab, it will reenter its hole. However, hermit crabs sometimes come up and touch a recently emerged *Ocypode* without the latter's paying the slightest attention. After some minutes' rest, during which some of the clinging sand has dried and fallen off, the crab cleans itself thoroughly, beginning with the polishing of the eyes with the palp of the third maxilliped. Not until almost an hour has passed do the largest crabs start toward the edge of the tide to feed. At first they walk slowly, then more rapidly, and at last gain their usual racing gait.

Feeding is carried on just in advance of the tide for an hour or more. Then the crabs return to the upper beach. (It is not yet certain that they return to the same holes they occupied during the preceding high water.) In any case each crab finds itself a burrow, which it repairs or enlarges according to its needs, or, rarely, it digs a new one. This work is punctuated with periods of feeding close to the hole. Sometimes there is still time after burrow repairs to feed at a distance again. Then the crabs gradually retire to their burrows, usually pulling in a plug of sand after them, until, fifty minutes to an hour before high tide, not a crab is left on the beach.

An interesting relationship was noted at Honda between the crabs and a nocturnal hermit

crab, not yet identified. This crustacean often was seen to come down from the jungle and enter the recently vacated hole of a beach crab, pull in a plug of sand, and spend the rest of the day, including, apparently, the succeeding high tide, if darkness did not fall before. *Ocypode* returning from the lower beach to find holes were never seen to pay the least attention to these newly occupied burrows, and no crabs appeared to be lost, or searching, in their vicinity. It may be that *Ocypode*, on broad beaches such as this, where they feed far from their holes, do not have a sense of property in regard to their burrows, once they have abandoned them after high tide, whereas crabs on narrow beaches, never straying far, may inhabit the same holes day after day.

O. gaudichaudii, as has been said, is active only during the day. In Panama City, on two nights, one brilliantly moonlit and the other dark, visits were made to the quite deserted beach where these crabs were numerous during the day. Although the holes had been opened by the crabs since the high tide (which fell after dark in each case), still not a crab had been feeding, as shown by the complete absence of pellets. The crabs themselves were usually found to be near the top of their sloping burrows, apparently asleep, since they were dug out without difficulty, whereas in daylight they always had to be dug from the very bottom of the long burrow.

The following is a typical time table of their daily activities, worked out from several days' observations on the broad beach at Bahia Honda. Sporadic observations made elsewhere agreed with these.

Hours After High Tide	
½	First young crabs emerge. (Since holes are not deep, tide leaves them first.)
1	First large crab emerges.
2	First large crab goes down to water's edge.
2–6	Migration of crabs to water's edge; the largest last, since they have deepest holes.
Hours Before High Tide	
3–1	Most crabs redigging holes and feeding intermittently around holes and at water's edge.
1	Last crab in hole. Largest are last to descend.

Obviously, this program can be carried out without postponement, interruption or curtailment due to darkness only when high tide is in the early morning or late afternoon. At Panama City, where there are exceptionally high tides, some members of a colony inhabited burrows which were not covered by neap tides. These individuals apparently spent most of their time quiescent in their holes during these periodic "droughts." More study is needed on this subject.

Material: In addition to the zoeae and megalopa recorded in a previous paper (Crane, 1940,[2] pp. 67, 70), a total of 55 specimens of *O. gaudichaudii* was taken by the Eastern Pacific *Zaca* Expedition in the following localities: Meanguera I., Gulf of Fonseca, El Salvador (Cat. No. 37,677); Corinto (37,736) and San Juan del Sur (3838), Nicaragua; Port Parker (3857), Port Culebra (38,141), Piedra Blanca Bay (38,198), Uvita Bay (38,442), Golfito (38,529) and Parida Island (38,651), Costa Rica; Bahia Honda (38,682), Panama; Gorgona Island (38,838), Colombia. In addition, 11 specimens were taken in Panama City, Panama, in February, 1941 (Cat. No. 4150).

Ocypode occidentalis Stimpson.

Text-figs. 3; 4 E, F; 5 A, C, E, G; 6 A, C; 7 A, B; Pl. II, Fig. 5.

References: Ocypoda occidentalis Stimpson, 1862, p. 229. *Ocypode occidentalis*, Rathbun, 1917, p. 372, pl. 129, figs. 2, 3; Rathbun, 1923, p. 632; Boone, 1929, pp. 562, 580, fig. 16; Crane, 1940, p. 70, text-figs. 3–8.

Range: Turtle Bay, west coast of Lower California, to Peru.

Local Distribution: Almost always found on unprotected beaches which are beaten by heavy surf. Occurs rarely on outer beaches somewhat protected by mud flats.

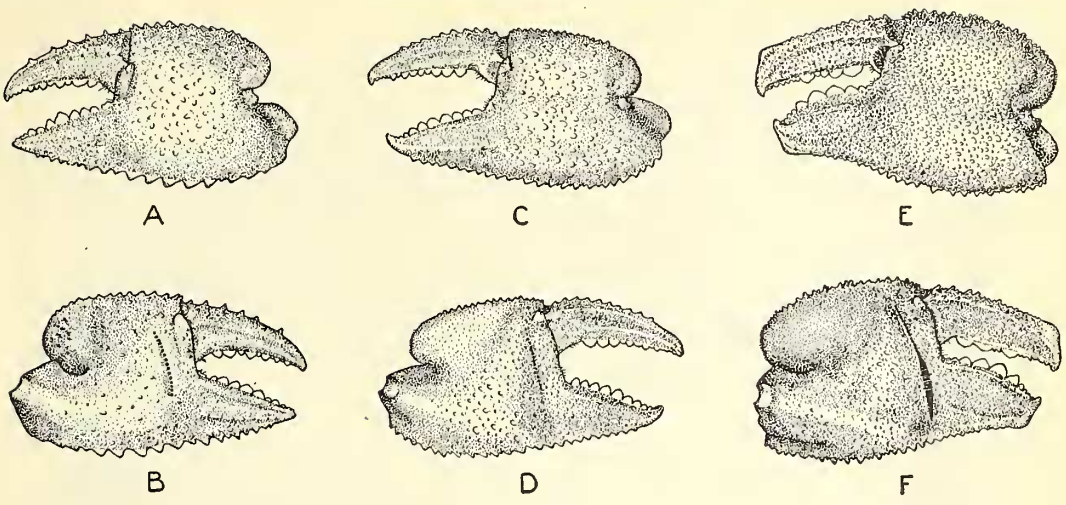
Size: The 35 specimens in the present collection measure between 3.9 and 24.5 mm. in length of carapace. The male co-type measured 43.2 mm. long.

Color: This species is much less highly colored than *gaudichaudii*, being always very pale, and always found on light sand. The carapace and legs of adults show marblings of gray and white on olive; the joint between merus and carpus of chelipeds is darkest, usually brownish; manus of chelipeds, all dactyls and underparts white.

The young are much more boldly patterned, with dark brownish-gray or even black marblings and splotches on olive buff. Legs banded irregularly with dark brown and gray. In the smallest there is a spot of scarlet in the middle of the posterior gastric region, and another on the merus of the last three pairs of ambulatories. In specimens of around 10 mm. in length, the red spots remain only on the gastric region and the most posterior ambulatory. In large crabs, measuring around 20 mm. or more, no trace of scarlet is found.

Early Crab Stages: Excluding the remarks concerning the specialized ocular stiles and chelae, the account of the young stages of *gaudichaudii* (p. 299 ff.) applies equally well to the present species, except that the stridulating ridge is not discernible in *occidentalis* until a length of about 6 mm. is reached. As shown in the key (p. 299), the young of the two forms may be distinguished

[2] In this paper reference was inadvertently omitted to Kemp's (1915) quotation of Annandale's notes concerning the behavior of the megalopa of *O. macrocera*. Dr. Annandale found that they made rudimentary burrows under the shelter of beached catamarans, became pale in strong light, and that they were preyed upon by adult crabs and, apparently, by ants. (Kemp, "Fauna of the Chelka Lake. Crustacea Decapoda." *Mem. Ind. Mus. Calcutta* 5, 1915, pp. 219–220, text-fig.)



Text-figure 7.

Major chelae of adult males in *Ocypode*. A, *occidentalis*, outer side; B, same, inner side; C, *albicans*, outer side; D, same, inner side; E, *guadichaudii*, outer side; F, same, inner side. All × 1.6.

by their coloration when alive and, when preserved, by the proportions of the ischium of the third maxilliped. From a phylogenetic point of view, it is interesting that in young *occidentalis* the orbital angles are even less advanced than in adults of the Atlantic species, *albicans*, although in adult *occidentalis* the reverse is true. Specimens measuring around 20 mm. in length appear to be mature. None of the few large specimens in the present collection seems to be near breeding condition.

General Habits: This species is clearly the analogue of the Atlantic *albicans*, and their habits turn out to be very similar, while utterly dissimilar to those of *gaudichaudii*. Like the Atlantic form, the present species is wholly nocturnal when adult, although the young are also active during the day. They are typical predators and scavengers at all ages.

The alimentary canals of twelve specimens were examined, from crabs measuring between 6 and 25 mm. in length, taken in eight different localities. The contents were distributed as follows: Amphipods were present in four specimens, beetles in four, seaweed in three, worms (setae and jaws) in two, Thysanura in two, a minute sea urchin in one, and one was empty. In four a few sand grains were mixed with the organic matter.

Material: In addition to the megalopa recorded in a previous paper (Crane, 1940, p. 70), a total of 35 specimens of *O. occidentalis* was taken by the Eastern Pacific *Zaca* Expedition in the following localities: Banderas Bay (Cat. No. 37,132), Chamela Bay (37,165), Tenacatita Bay (37,199), Acapulco (37,278), and Port Guatulco (37,445), Mexico; Gulf of Fonseca near Potosi River (37,702) and Corinto, Nicaragua; Port Culebra (38,125), Costa Rica; Bahia Honda (38,698), Panama.

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EXPLANATION OF THE PLATES.

Plate I.

Fig. 1. *O. gaudichaudii*. Buccal frame of adult female, carapace length 25 mm. E marks enlarged endite of first maxilliped. Bahia Honda, Panama. × 3.5.

Fig. 2. *O. occidentalis*. Buccal frame of adult female, carapace length 24.5 mm. Port Guatulco, Mexico. × 3.5.

Plate II.

Fig. 3. *O. gaudichaudii* beside burrow, with heap of excavated sand, feeding pellets and scraping marks of truncate chelae. Bahia Honda, Panama.

Fig. 4. *O. gaudichaudii*. Right abdominal appendage, right lateral view. Carapace length 25 mm. Panama City, Panama. × 6.6.

Fig. 5. *O. occidentalis*. Right abdominal appendage, right lateral view. Carapace length 25 mm. Chamela Bay, Mexico. × 9.2.

Fig. 6. *O. albicans*. Right abdominal appendage, right lateral view. Carapace length 24.5 mm. Bermuda. × 6.4.